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Chapter 7

Some Observations from Two Coyote-Prey Studies

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ABSTRACT

Results from 2 long-term field studies of coyote-prey interactions are used as a basis for discussing aspects of predation and the impact predators may have on prey populations. In one study, coyotes (*Canis latrans*) were identified as a proximate cause of death to a high proportion of white-tailed deer (*Odocoileus virginianus*) fawns. Subsequent analyses revealed that variations in natality as well as fawn survival rates were linked with precipitation patterns in preceding months. Ultimately, a coyote exclosure experiment resulted in a population irruption of deer within the exclosure followed by decline to pre-exclosure densities, but with the deer in a much less vigorous condition. A separate demographic study of a cyclical population of black-tailed jackrabbits (*Lepus californicus*) suggested that predation, primarily by coyotes, may be an important factor in the cyclical nature of that population. A mathematical model developed from the field data suggests that further investigation of the assumptions and implications of these interpretations is warranted. Some of the problems associated with studying and interpreting information related to the impact of predators upon prey populations are discussed.

INTRODUCTION

Predation is a common component of most natural biological systems. Evolution has equipped various taxa with physical, physiological, and behavioral characteristics enabling them to survive by stalking, chasing, capturing, and killing other animals. While acts of predation are readily documented, the biological significance of such events is not well understood. Few studies of vertebrate predator-prey interactions have produced unambiguous assessments of the impacts predators have on prey populations. Studies of interactions between coyotes and their prey are no exception.

We have been involved with 2 intensive empirical studies of coyote-prey interactions and will use information gleaned from them as a basis for this discussion. The first involves coyote predation upon white-tailed deer on the Welder Wildlife Refuge in southern Texas and the other relates to coyote-jackrabbit interactions in Curlew Valley, Utah.

THE WELDER COYOTE-DEER STUDIES

The Welder Wildlife Refuge (WWR) is a 31.6-km^2 experimental grazing and wildlife research ranch on the Gulf Coast of southern Texas. White-tailed deer are abundant (25-35/km^2) on this area, are not hunted for sport, and have been intensively studied for more than 30 years (Knowlton 1964, 1976; White 1966; Cook et al. 1971; Kie 1977; Kie and White 1985; Teer et al. 1991). Coyotes are also abundant (0.5-1.0/km^2; Teer et al. 1991), and various aspects of their biology, behavior, and interactions with deer also have been studied (Knowlton 1964; Kie et al. 1979; Andelt 1982, 1985; Andelt et al. 1987). We draw upon these studies as background.

Coyote Food Habits

Mammals compose 80 percent of the annual diet of coyotes on the WWR. Wild fruits and insects each compose about 10 percent of the annual diet but contribute 30-80 percent of the diet on a seasonal basis (Andelt et al. 1987). Fruits like dewberry (*Rubus trivialis*), agarito (*Berberis trifoliata*), and lotebush (*Condalia obtusifolia*) are available late March through May, while prickly pear (*Opuntia lindheimerii*) and Texas persimmon (*Diospiros texana*) ripen July through September. Insects were only common in the diet from late summer until late November. The mammalian component of the diet is composed mainly of white-tailed deer, rodents, and lagomorphs. Although deer are common in the diet throughout the year, they are most common in winter (60 percent of the diet) and June through July (70 percent of the diet) (Figure 1). Documentation of these trends spans 18 years (Andelt et al. 1987).

Fawn Mortality

The high incidence of deer in the coyote diet during June and July coincides with the fawning and early postnatal period and suggests this may be a vulnerable period for deer and a period of particular interest for assessing the impact of coyotes on deer demography. Comparing fetal counts with doe-fawn ratios between 1962 and 1979 suggests a mean survival rate of 34 percent (range = 11-49 percent) during the first year of life (Kie and White 1985). Two sources of information indicate most fawn deaths occur in the first 3 weeks of life. First, 95 percent of 174 fawns found dead were less than 3 weeks of age at death. Second, minimum survival estimates determined from sightings of tagged fawns (n = 125) indicated only 25 percent were known to be alive after 3 weeks of age (Knowlton 1964, 1976). Subsequent radio-telemetry studies by Cook et al. (1971) demonstrated over 50 percent of the neonatal mortality involved fawns killed by coyotes. This suggests that in the absence of sport hunting, coyote predation on fawns was a major mortality factor and potential constraint on the deer population.

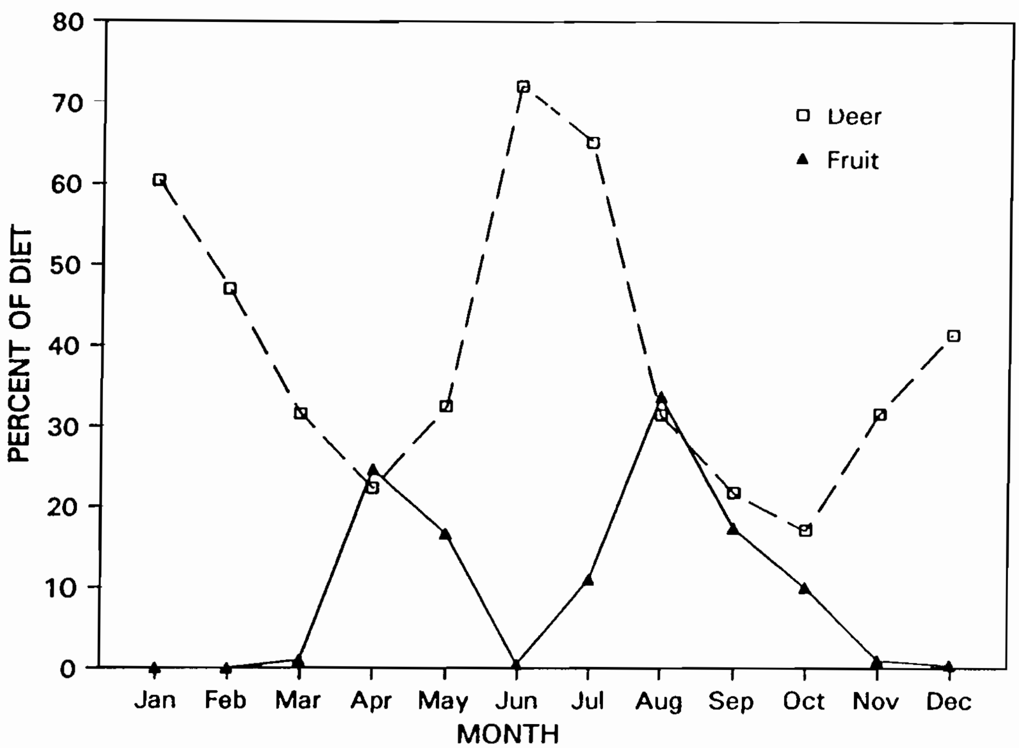

Figure 1. Relative contribution of deer and fruit to the seasonal diet of coyotes on the Welder Wildlife Refuge, Texas.

Deer Demography

Knowlton (1964, 1976) suggested deer fecundity and fawn survival rates were linked to the amount of precipitation during periods as much as 12 months preceding fawning. Kie and White (1985) reaffirmed these interpretations, and suggested fawning was more synchronous and possibly advanced as much as 12 days when precipitation was above average. Interestingly, survival among male fawns was generally half that of female fawns. Consequently, explanations of the variations in predation rates on

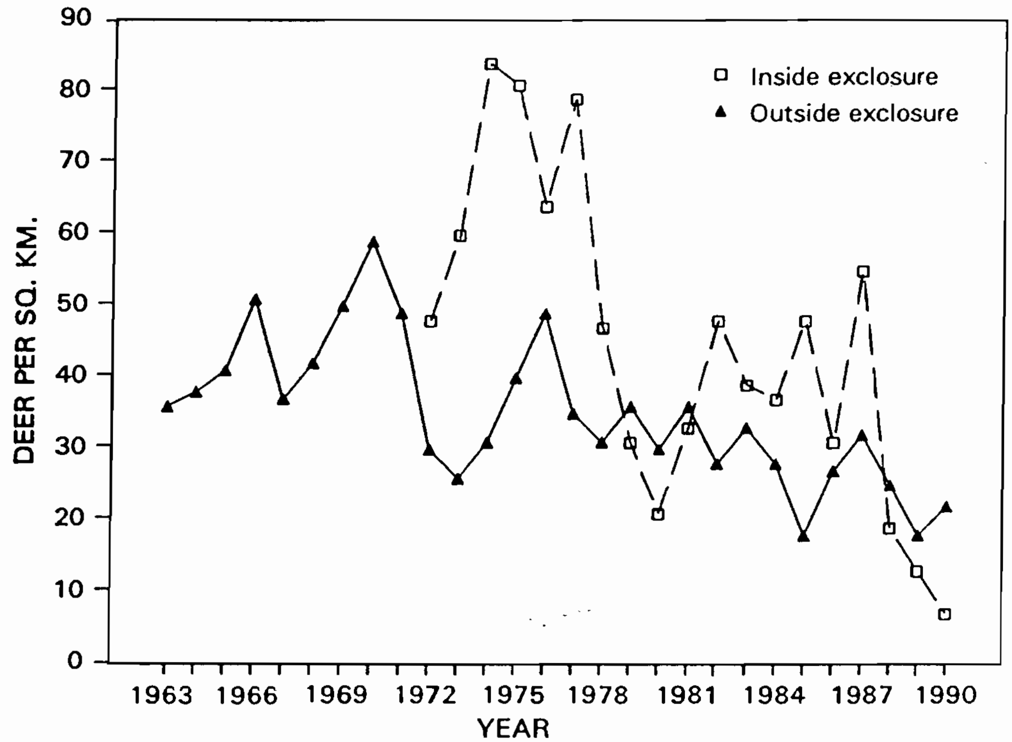

Figure 2. Estimates of deer densities inside and outside a coyote exclosure on the Welder Wildlife Refuge, Texas (adapted from Teer et al. 1991).

fawns on the WWR must incorporate precipitation patterns in the months preceding fawning as well as a predisposition for coyotes to kill male fawns.

Our current interpretations suggest that precipitation during the previous summer affects conception and fecundity among the deer through the quantity and quality of available forage. When precipitation has been above average, there typically is a 10+-day advance in fawning, with a concomitant spike in the fraction of fawns born early. This results in many fawns born while spring fruits are still available on the WWR and coyotes are conditioned to feeding on fruit (Figure 1). Subsequently, precipitation during gestation presumably influences the quantity and quality of forage, which in turn affects the size (Knowlton et al. 1979), and presumably health, of fawns born and likely the lactation rates of does as well. Conversely, when precipitation has been low and the amount and quality of forage is reduced, smaller fawns are born later to does that are less capable of nurturing them. Seeing fawns wandering and bleating, apparently seeking their dams, is not uncommon in such situations. Such actions should provide effective cues for coyotes. In scenarios where nutrition appears to assume a major role, we might anticipate that male fawns, which typically grow faster (Knowlton et al. 1979) and are more active than female fawns (Jackson et al. 1972), would be placed in greater jeopardy and be more vulnerable to predation than male fawns.

Coyote Exclusion Studies

Despite a preponderance of evidence suggesting high levels of coyote predation on young fawns, the net impact of coyotes on deer demography remained undefined until a 391-ha exclosure was built and coyotes inside the exclosure were systematically removed to greatly reduce densities (Kie et al. 1979; Teer et al. 1991). After the initial coyote removal, additional coyotes were removed whenever evidence of their presence was noted. Deer densities within the exclosure subsequently tripled compared to outside, remained stable for 2-3 years, and then declined precipitously to levels only slightly above those recorded outside the exclosure (Figure 2). Forage for deer within the exclosure deteriorated significantly (Kie and White 1985; Teer et al. 1991). The general health of the deer declined noticeably and parasite loads increased. Ultimately, the decrease in early postnatal mortality was compensated by increased mortality among fawns 6-12 months of age. Coyotes clearly were affecting survival of young deer. The removal of fawns by coyotes at earlier ages apparently helped maintain the remaining herd in much better physical condition.

In summary, in the absence of predation, herd numbers increased pending development of other constraints. In this case, the alternate constraints (i.e., malnutrition and parasitism) returned the deer herd to similar densities as before but in a much less thrifty condition.

THE CURLEW VALLEY COYOTE-JACKRABBIT STUDIES

Black-tailed jackrabbits are the most abundant medium-sized herbivore throughout much of the Great Basin area of western North America, including Utah. Similarly, coyotes are the dominant carnivore and principal mammalian predator on adult jackrabbits in this area. In 1962, Frederic Wagner initiated demographic studies of the black-tailed jackrabbits in Curlew Valley in northern Utah (Gross et al. 1974; Wagner 1981). Studies of coyotes were added a few years later (Clark 1972; Knudsen 1976; Hoffman 1979; Davison 1980). Some of these studies are still in progress. The accumulated information now constitutes a unique vertebrate predator-prey data set because some aspects of the studies have continued for nearly 30 years.

Jackrabbit Population Aspects

Densities.—About 70 1-mile flushing transects that have run each spring and fall since 1962 provide indices of jackrabbit abundance in a 640 km^2 portion of Curlew Valley (Gross et al. 1974). Jackrabbit numbers fluctuated in a cyclical manner with 30- to 50-fold changes in abundance and population peaks in 1970, 1981, and possibly 1992 (Figure 3). This cyclical pattern in jackrabbit abundance is common to a broad region of the inter-

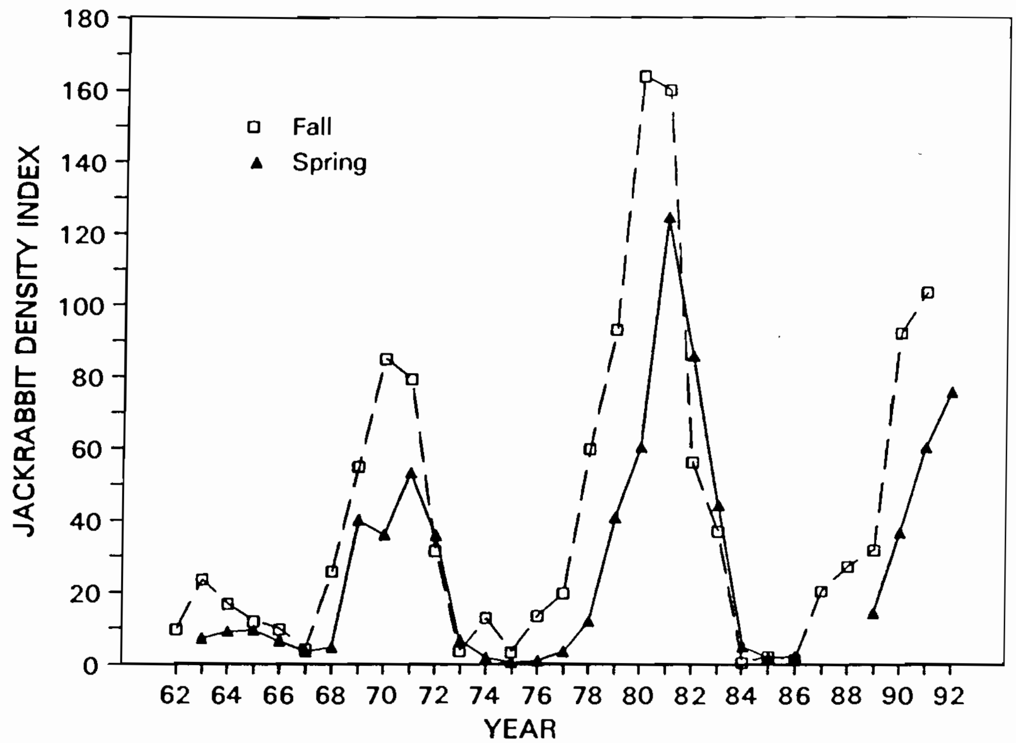

Figure 3. Spring and fall indices of jackrabbit abundance in Curlew Valley, Utah, 1962-91.

mountain area (Stoddart 1987a, b; Eberhardt and Voris 1988; Knick 1990). In both instances of population decline, negative population growth first appeared in fall rather than spring. From this, we infer that initiation of the decline occurred between mid-spring and mid-fall, and probably resulted from a substantial decrease in recruitment to the adult population.

Reproduction.—Between 1962 and 1984, collection and necropsy of female jackrabbits throughout the reproductive season provided a measure of productivity within the population. Typically, jackrabbits in this area produce 4 litters per year, with mean litter sizes of 1.6, 4.5, 5.0, and 4.0 respectively as the year progresses (Gross et al. 1974). To determine whether the apparent decreased recruitment resulted from an intrinsic density-dependent factor, we regressed the annual natality rate against jackrabbit density (Figure 4). A slight negative density-dependent trend ($r^2 = 0.21$) was evident ($P = 0.05$) but was inadequate to account for the magnitude of density changes noted.

Mortality.—Estimates of over-winter mortality of adults were determined by comparing fall and spring density estimates. Over-summer mortality estimates were determined by applying age ratio data from jackrabbits collected in the fall to population estimates for fall so that density estimates of juvenile and adult jackrabbits could be calculated. We then compared (1)

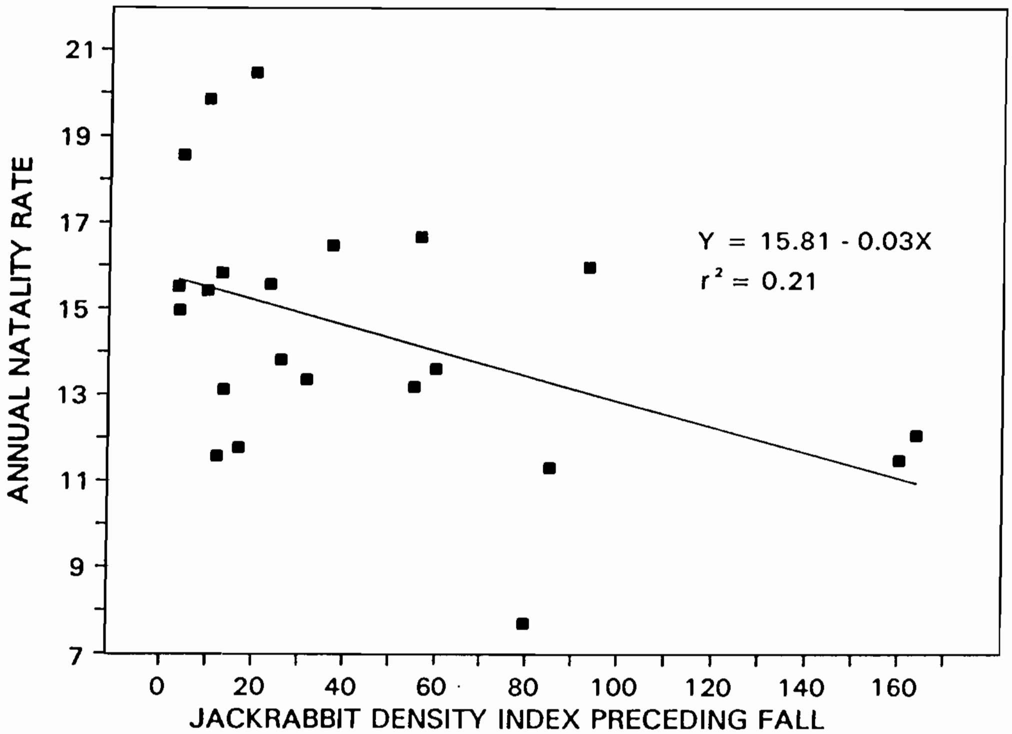

Figure 4. Jackrabbit natality rate in Curlew Valley, Utah, in relation to jackrabbit density the preceding fall.

the spring density estimate with the calculated density of adults in fall to determine the over-summer mortality of adults, and (2) the natality estimate with the calculated density of juveniles in fall to estimate the birth to fall mortality of juveniles. An inverse relationship between mortality rates, k-values (Varley and Gradwell 1960), of both juvenile ($r^2 = 0.70$, $P \leq 0.005$) and adult jackrabbits ($r^2 = 0.88$, $P \leq 0.005$) with population trend is apparent (Figure 5), suggesting a close relationship between the trend in jackrabbit abundance and jackrabbit mortality rates. These analyses, however, are subject to problems associated with auto-correlation because calculations for mortality rates and population trends both used density data.

Cause of death among jackrabbits was estimated from the fates of 444 jackrabbits equipped with motion-sensitive radio transmitters during 5 monitoring periods (Smith 1987). The 30-day mortality rates within the population increased from 0.05 to 0.20 during the irruptive and early decline phases of the cycle, peaked at 0.42 during the late decline phase, and dropped back to around 0.20 immediately thereafter (Figure 6). Predation was a common cause of mortality (48-82 percent of mortalities recorded during individual monitoring periods) and accounted for much of the variation noted in jackrabbit mortality rates.

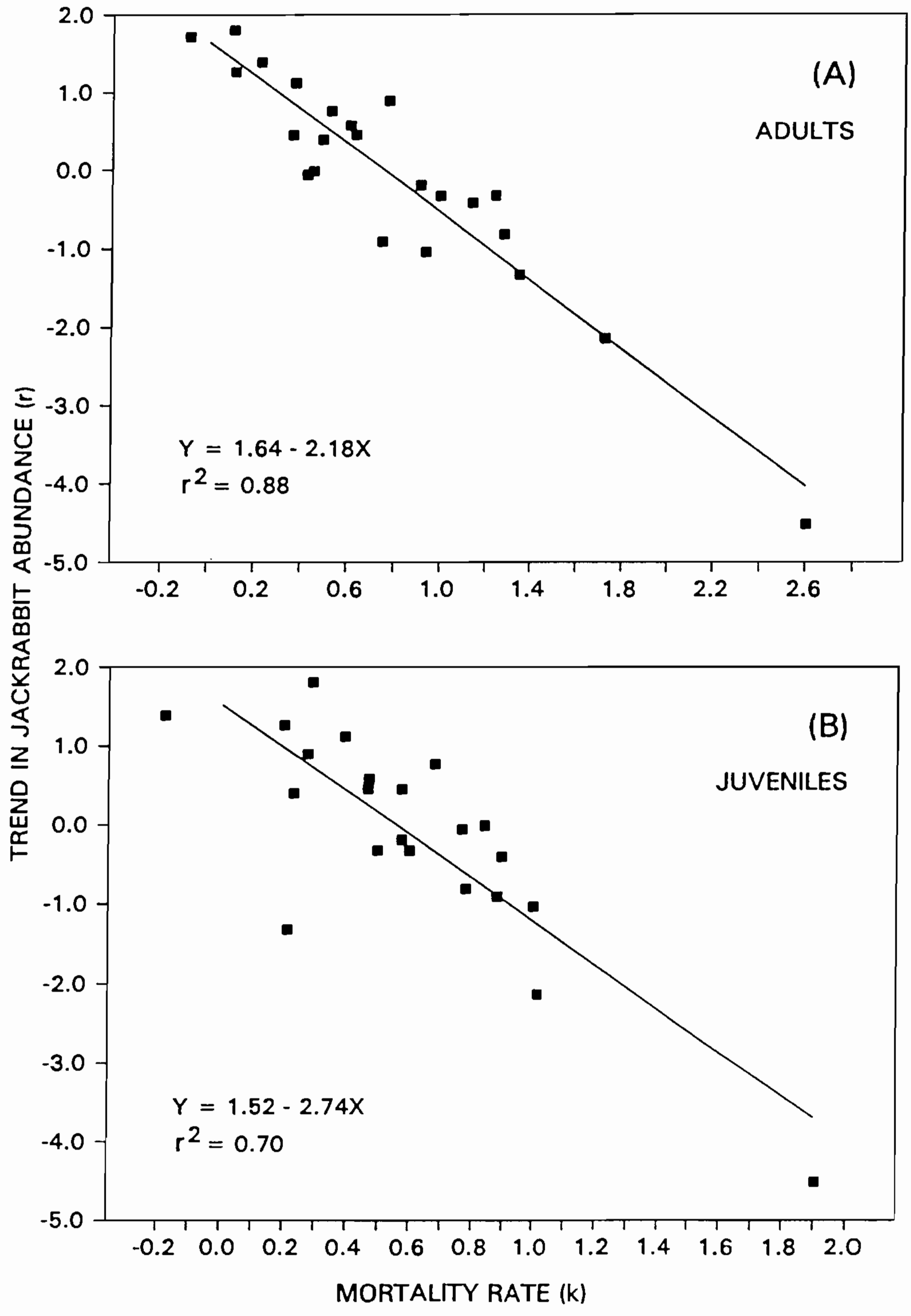

Figure 5. Jackrabbit population trend in Curlew Valley, Utah, as a function of (A) fall to fall adult jackrabbit mortality rates (k_a) and (B) birth to fall juvenile jackrabbit mortality rates (k_j).

Coyote Aspects

Densities.—Coyote population trends in Curlew Valley were determined in spring and fall via various indices, including catch-per-unit-effort, scent station visitation rates, and scat deposition rates (Clark 1972; Davison 1980; Roughton and Sweeny 1982). Values from each indexing technique were normalized and then averaged to provide a single density index value for each spring and fall of each year. Coyote abundance varied more than 10-fold between trough and peak populations. Density fluctuated in general synchrony with the abundance of jackrabbits with a phase difference of 1-2 years between peak abundances of the 2 species (Figure 7).

Coyote Feeding Patterns.—Studies by Clark (1972), Hoffman (1979), and others suggest jackrabbits compose a major portion of the coyote diet even when jackrabbits are relatively scarce (Figure 8). Hence it was not surprising that coyote densities appeared to be responsive to changes in jackrabbit abundance.

Supplemental Analyses.—Our data suggest coyotes are a major component in the cycle of jackrabbit abundance but interpretations are far from conclusive. At this point, our analytical attempts took two directions. We first assessed the degree to which the cyclical pattern of jackrabbit abundance was associated with intrinsic factors within the jackrabbits compared to factors associated with coyote abundance. To do this, we plotted the annual change in jackrabbit abundance (r) first as a function of fall jackrabbit density and then as a function of fall coyote abundance. In the first case, a somewhat circular pattern, or phase plane, emerged for both the first and second cycles (Figure 9a). This suggests that either a time-delay or some factor other than jackrabbit density was involved. While the overall relationship between coyote abundance and jackrabbit population change at first appeared ambiguous, linear relationships emerged when the data for individual cycles were regressed independently (Figure 9b). Linear aspects of the relationship suggests the possibility of causality, but the apparent difference between the 2 cycles remains unexplained. Although these analyses are not definitive, they provide a suggestion that factors related to coyote abundance may be more important in the cyclical nature of the jackrabbit population than some intrinsic, density-dependent factor among the jackrabbits.

Coyote-Jackrabbit Interaction Model

A second analytical approach involved formulating an empirical predator-prey interaction model based upon the data collected in the field. From the outset, we recognize that a model that mimics the field situation neither proves nor disproves the relationships that are incorporated, but to a degree it helps assess the plausibility of explaining the documented patterns with the assumed relationships. We used information collected in the first 22 years of

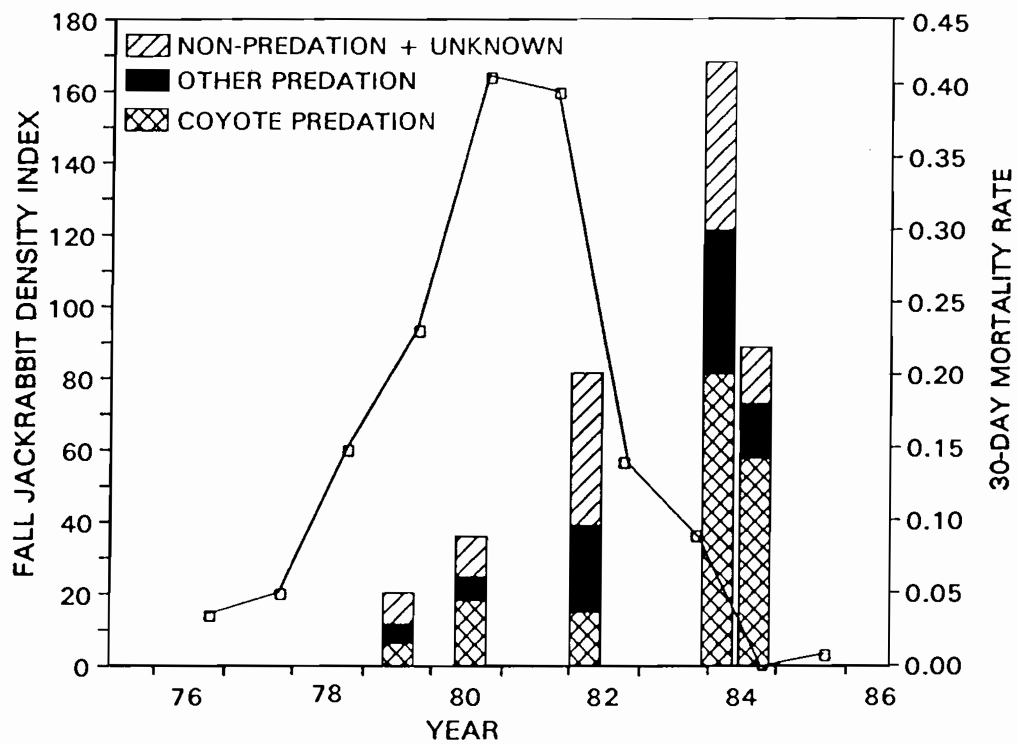

Figure 6. Rates and causes of mortality among 444 radio-instrumented jackrabbits (bars) in Curlew Valley, Utah, during 5 monitoring periods in relation to cycle of jackrabbit abundance (line) (adapted from Smith 1987).

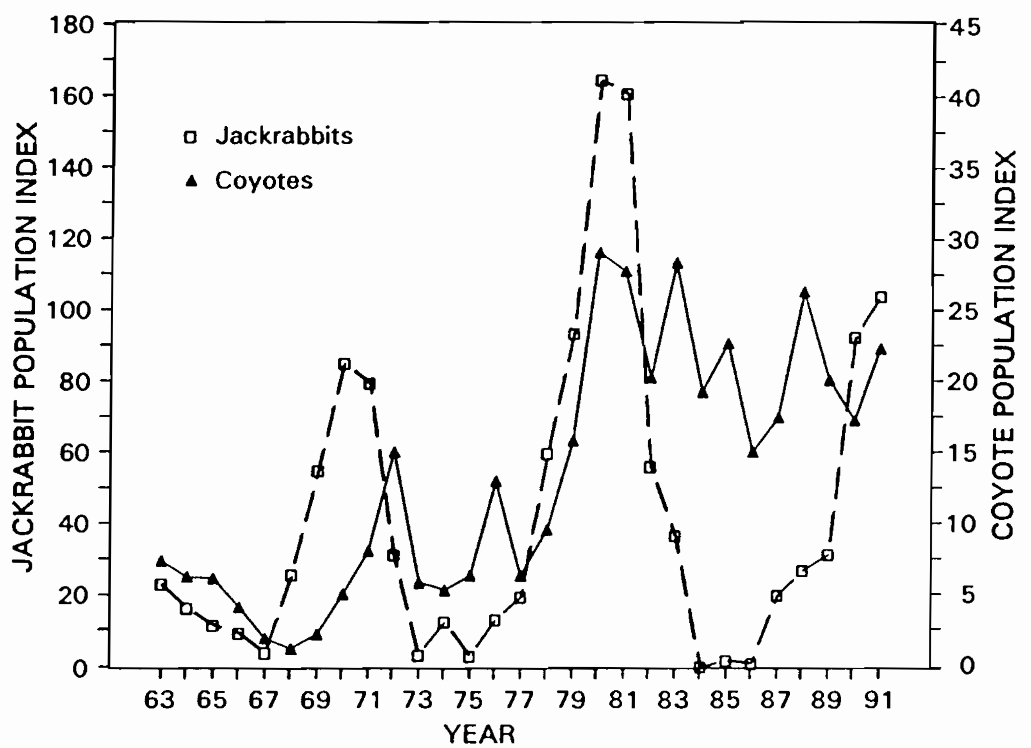

Figure 7. Fall indices of coyote and jackrabbit abundance in Curlew Valley, Utah, 1962-91.

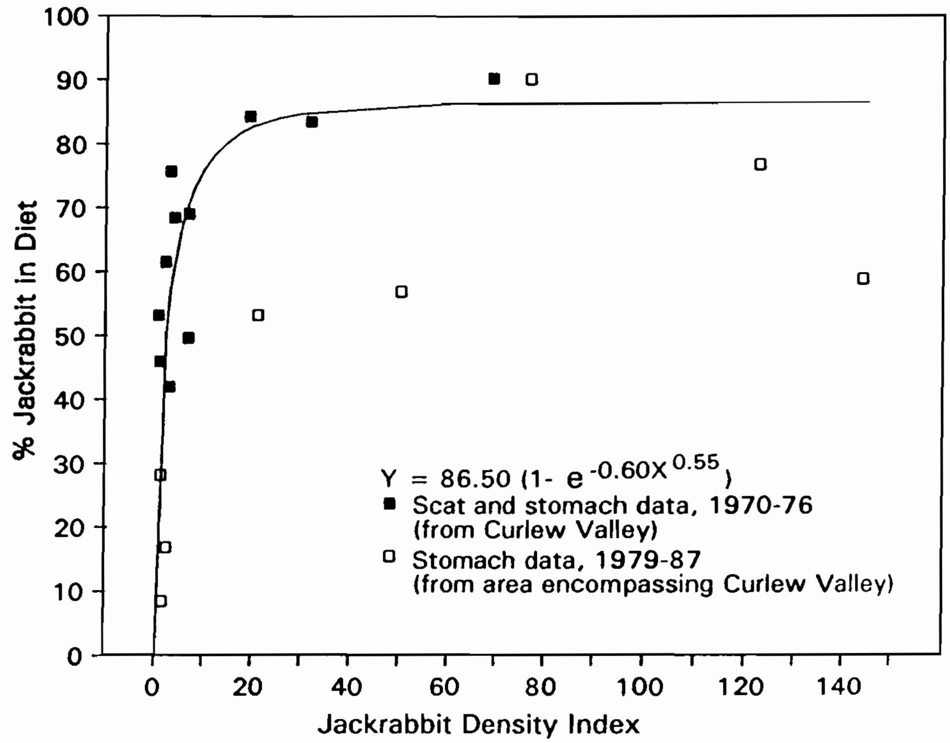

Figure 8. Functional feeding response of coyotes in Curlew Valley, Utah, to changes in jackrabbit abundance.

the study (failure to obtain annual reproductive data in subsequent years precluded calculation of juvenile and adult survival rates) to develop 4 equations which were then combined in a 9-step process representing each annual cycle. Each time-step in the model equates with 40 days, with time-step 1 starting in November. The equations represent (1) coyote population change, (2) jackrabbit natality, (3) adult jackrabbit mortality, and (4) juvenile jackrabbit mortality. Each will be discussed individually.

Equations.—The change (r) in coyote abundance appears to be almost a step function of jackrabbit abundance (Figure 10). When the jackrabbit abundance index is above 20, the coyote population quickly reaches an asymptotic rate of increase of 0.6. We approximated this relationship with the equation:

$$\text{Coyote } r = 0.6 - 1.6e^{-0.006\,(\text{rabbit index})^{1.8}}$$

In the model, coyote density changes were updated in time-step 9 of each annual period.

Jackrabbit natality was incorporated into the model each year as a function of each female calculated to be alive during time-steps 3, 4, 5, and 6 producing litters with 1.6, 4.5, 5.0, and 4.0 young in the respective time-steps.

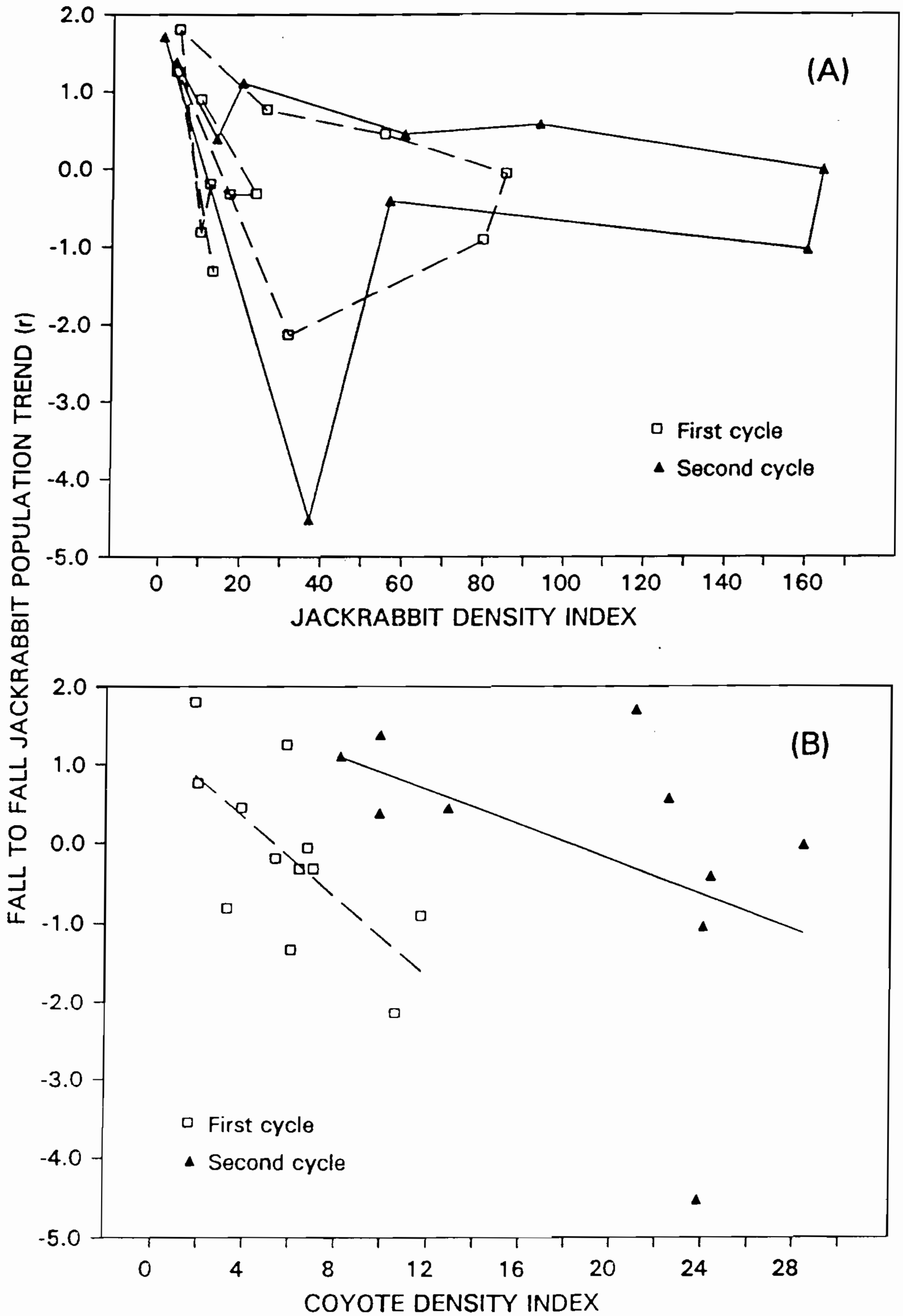

Figure 9. Trend in jackrabbit abundance in Curlew Valley, Utah, in relation to (A) the jackrabbit density index the previous fall and (B) relative coyote abundance (density value = mean of index values at beginning and end of respective year).

The modest density-dependent aspects noted in jackrabbit natality were not incorporated into the model.

Equations for both juvenile and adult jackrabbit mortality were derived only from years of irruption and decline when hares were fairly abundant (mean of fall and spring indices ≥15). This was done to avoid generating spurious information when the hare population was low and large sampling errors were likely. Since capturing adult jackrabbits is likely a strenuous task, we assumed coyotes hunt for adult jackrabbits when hungry, but after catching one are unlikely to hunt for additional adult jackrabbits until they become hungry again. If this assumption is correct, the impact of coyotes on the adult portion of the jackrabbit population (Figure 11) is a function of both the number of coyotes (direct) and the number of jackrabbits (inverse). This equates to a coyote-rabbit ratio (C/R). The adult jackrabbit mortality rate (k_a) was approximated by:

$$k_a = 0.35 + 1.50\ (C/R)$$

Adult jackrabbit mortality was updated during each time-step of the model.

Small jackrabbits, however, try to escape by hiding and can be easily caught once they are detected. Coyotes may not actively seek juvenile jackrabbits because they are difficult to locate and constitute inadequate meals, but likely kill them whenever they are encountered incidental to other activities. In essence, we hypothesize that in routine activities, each coyote traverses a transect and kills the juvenile jackrabbits detected. This implies that each coyote kills a constant fraction of the juvenile jackrabbits in the population, and the accumulate fraction of juvenile jackrabbits killed is strictly a function of the number of coyotes. Although the juvenile mortality rate appeared linear with regard to coyote abundance, somewhat different relationships existed during the two cycles for which we had data (Figure 12), suggesting other factors were involved. For the model, we represented juvenile mortality (k_j) with an intermediate equation:

$$k_j = 0.39 + 0.024\ (\text{coyote index})$$

The number of juveniles in the model population was appropriately adjusted during time-steps 4-9. Juvenile jackrabbits surviving through time-step 9 of the model became adults.

Each of the foregoing equations was converted to a 40-day rate and entered into our predator-prey interaction model at appropriate time-steps within each model year.

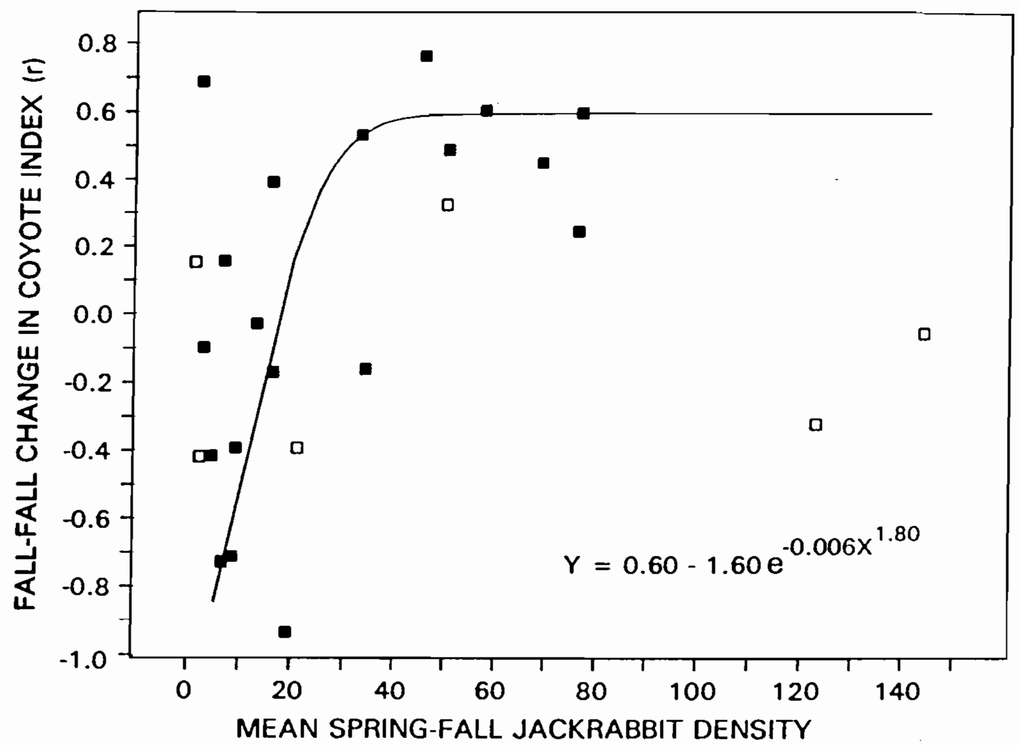

Figure 10. Change in coyote abundance in Curlew Valley, Utah, in relation to jackrabbit abundance (open squares = 1981-86 when coyote density apparently stabilized due to constraints other than prey abundance; see Fig. 7).

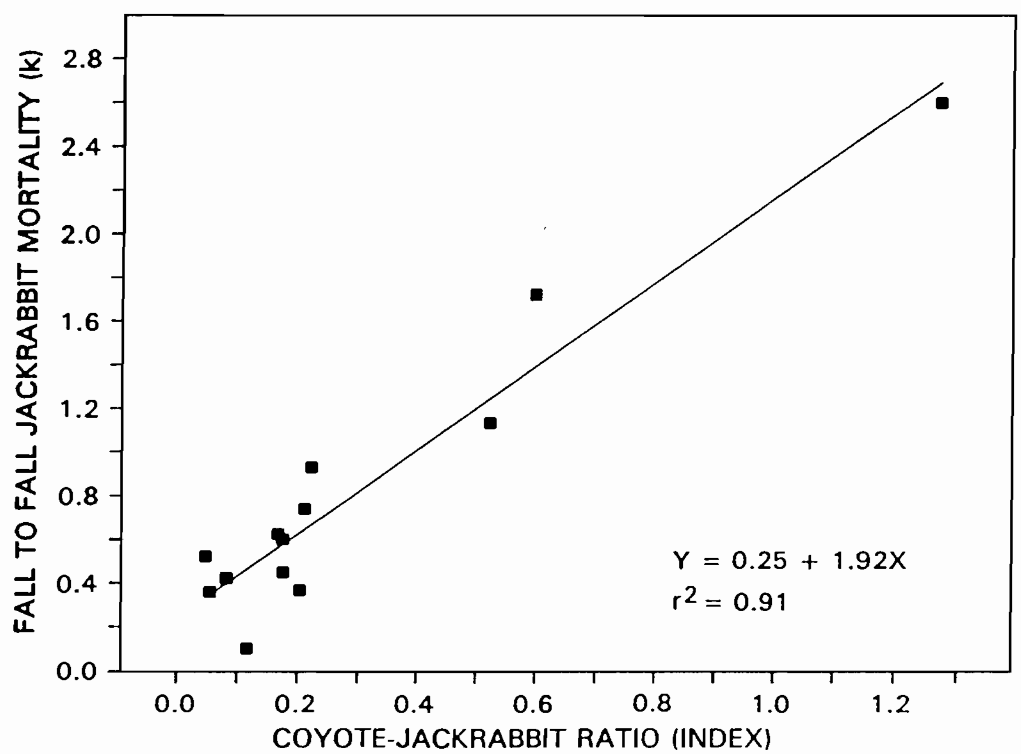

Figure 11. Adult jackrabbit mortality in Curlew Valley as a function of coyote-jackrabbit ratios (only years when mean jackrabbit index exceeded 15 are included).

Model output.—During initial runs, the model output resulted in the jackrabbit population becoming extinct or becoming infinitely large, forcing us to reconsider the model and the data. We subsequently placed two constraints on the model to incorporate seemingly realistic biological assumptions. The first allowed jackrabbit abundance to go to very low numbers but not to extinction, trying to mimic the likelihood that ingress would always provide a nucleus for the jackrabbit population. The other placed an upper limit on coyote numbers, representing invocation of an additional constraint on coyote abundance, such as coyote territoriality placing a "ceiling" on coyote density in the area. This appears reasonable because in 1981 and 1982 coyote abundance became static at a time when jackrabbit densities were still high (Figure 7 and 10) and coyote densities might normally be expected to increase.

Incorporating these constraints produced a model output (Figure 13) with several interesting characteristics: (1) there was resilience within the model and we could start the model with any combination of coyote and jackrabbit densities and within 3 cyclical oscillations the output stabilized in a cyclic pattern; (2) jackrabbit abundance reached a peak at approximately 10-year intervals; and (3) peak jackrabbit abundance varied appreciably on successive cycles. Fabricating a model with an output that has characteristics similar to field observations is not a validation of the model. It does, however, suggest it is not unreasonable to continue exploring inferences related to such a model.

Several caveats should be mentioned. Our model utilized single predator-single prey equations. While the Curlew Valley ecosystem is relatively simple, it is not this simple. Coyotes are not the only predator nor jackrabbits the only prey. Coyotes are, however, the principle mammalian carnivore and arguably provide a reasonable index of abundance within the predator complex impacting the jackrabbit population. Second, the model does not incorporate influences from other prey species. Jackrabbits are the dominant herbivore and principle prey species, especially during winter. Potential changes in factors that might change predator ability to exploit prey populations (e.g., learning, conditioning, etc.) have not been incorporated into the model. Nor does the model incorporate any tertiary mortality factors impacting predator numbers (e.g., human influence on the coyote population).

Data collected since 1984 have created reservations about the suitability and utility of the model. Two aspects noted since the peaks in hare and coyote abundances were documented in 1980 and 1981 warrant mention: (1) the coyote population did not decline as expected with the demise of the jackrabbits, and (2) the jackrabbit population irrupted during 1987-92 at a time when it might not have been anticipated based on indices of coyote

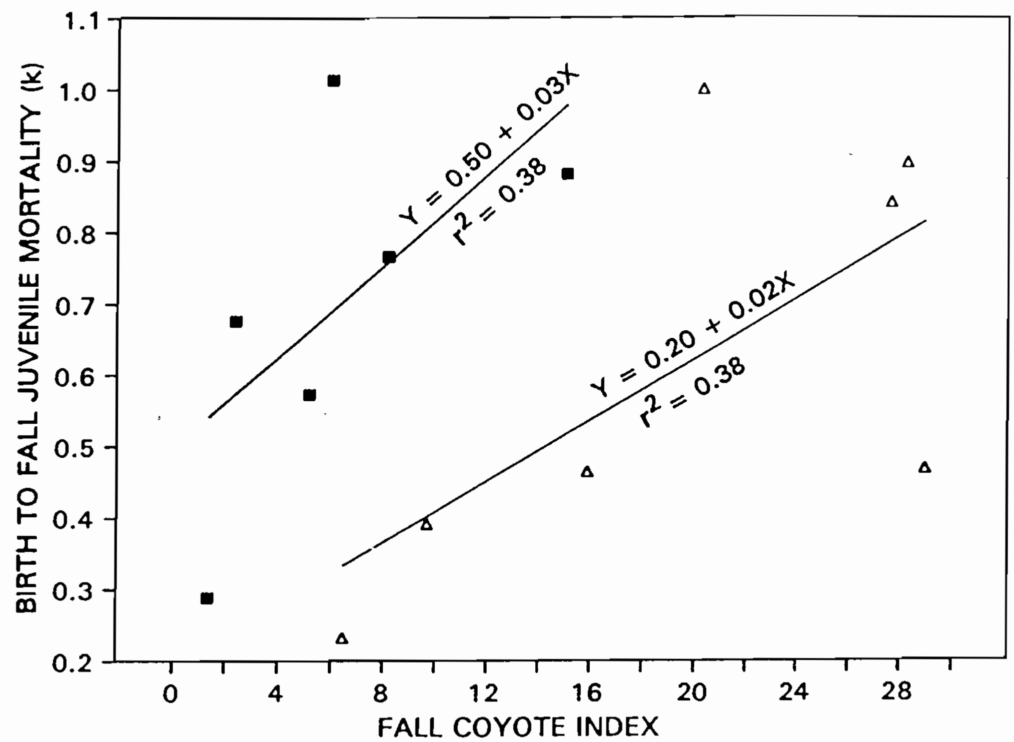

Figure 12. Juvenile jackrabbit mortality in Curlew Valley as a function of the fall coyote index (only years when mean jackrabbit index exceeded 15 are included).

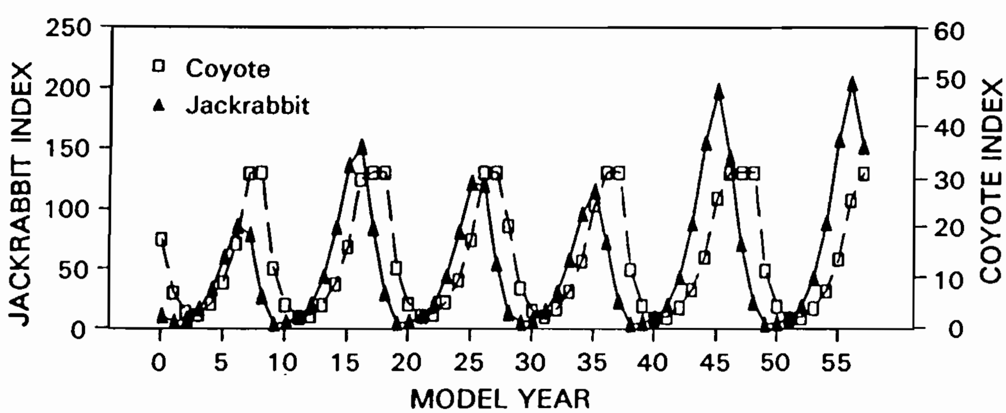

Figure 13. Output from coyote-jackrabbit population interaction model covering 57 "annual" (9-step) cycles.

abundance and our equations regarding jackrabbit mortality. The persistence of high coyote numbers during this period could be explained by marked increases in alternate winter prey, especially wild ungulates, or suspected changes in coyote harvest rates associated with low pelt prices. Similarly, the irruption of jackrabbits in the face of high coyote densities might be attributable to erroneous assumptions about the merit of using coyote abundance as an index to what was happening within the predator complex affecting jackrabbits, or perhaps important changes in hare distribution resulting from a range fire that destroyed jackrabbit resting cover over more than 30 percent of the study area in 1984. Such rationalizations, however, easily distract from the purpose and utility of the model and do not provide additional insights to species interactions.

DISCUSSION

Interests in predator-prey relationships frequently originate amid concerns for one or more species identified as potential prey. Attempts to assess the role or impact of predators has traditionally started with studies of feeding patterns. Not surprisingly, the predators are often found feeding upon the species of concern, frequently to a surprising degree. In the studies presented here, white-tailed deer composed an important part of the coyote diet on the Welder Wildlife Refuge and jackrabbits were the single most important prey of coyotes in Curlew Valley. While such studies may suggest something about the importance of prey to the predator, and perhaps the seasons and life stages in which the prey were vulnerable, they said little about the impacts predation had on prey populations. Prey populations that composed large fractions of the predator's diet frequently appear sufficiently resilient and capable of accommodating substantial predatory losses, while other species that are relatively scarce and make very minor contributions to predatory diets may be dramatically impacted by predation. In the latter case, for example, studying predator feeding patterns may not detect consumption of 5 whooping crane (*Grus americana*) chicks, but the loss might dramatically impact the whooping crane population.

Subsequently, scientific inquiry directed attention toward identifying and interpreting predator-caused losses within the composite population processes of the prey. In the Welder studies, we suspect that coyotes were the proximal cause of a high proportion of fawn mortality but their impact was mediated by other factors, primarily precipitation patterns in preceding months. On the other hand, it appears plausible that predation might be a major factor in the cyclical pattern of jackrabbit abundance in Curlew Valley. The coyote-jackrabbit paradigm presented is but one of several hypotheses that might account for the patterns observed. Its validity, or that of any hypothesis or model, can only be determined by appropriate tests.

We now recognize that a definitive understanding of the influence predators have on prey abundance requires perturbation of predator numbers. In the case of the Welder deer herd, a dramatic increase in survival rates and deer numbers immediately followed a radical decrease in predator abundance. The increase now appears to have been temporary in nature and achieved at the expense of the general health and vigor of the surviving animals. In the absence of predation upon young fawns, early postnatal survival and deer density increased, and ultimately was followed by forage depletion, malnutrition, loss of health and vigor, and eventual population decline. If we had simultaneously enhanced mortalities from other causes, such as hunting, interpretations might be different.

We are reluctant to speculate about effects that might be associated with reducing coyote predation on jackrabbits in Curlew Valley. Without more pertinent information, it remains conjectural whether the jackrabbit population would continue in cyclical patterns of abundance; whether the long-term average abundance would increase or decrease; or what alternate constraints would eventually place limitations on hare abundance.

Our current interpretations of the Curlew Valley data also suggests it is plausible that predation on various life stages of prey may be functionally different, depending upon the frequency with which individuals may be caught, the effort the predatory act requires, and qualitative and quantitative nutritional aspects provided by captured prey. There obviously is much yet to be learned.

Some Research Perspectives

Like most scientific endeavors, inquiry into predatory relationships starts with descriptions and the cataloging of natural events. Much of the information provided here regarding coyote interactions with deer and jackrabbits involves such descriptions of demographic information. Interpretations of such information results in models, the propriety of which can be determined only through careful scrutiny and testing. For white-tailed deer on the WWR, the exclosure provided one test of a verbal model. In the case of the Curlew Valley studies, we developed, but did not test, a quantitative model of coyote-jackrabbit interactions. Both situations deserve more careful scrutiny of the information, detailed identification of competing explanations (hypotheses), and development of tests designed to clearly delineate among them.

Such tasks are difficult. Conducting activities on a meaningful scale can be intimidating and, as in the case of the coyote-jackrabbit cycle, appropriate test conditions may occur infrequently (perhaps only at 10-year intervals).

Obtaining and maintaining the mental, political, and economic support for such endeavors is a consideration of its own. Analyses of our coyote-jackrabbit studies suffered from small numbers during low jackrabbit abundance (70 1-mile transects were not sufficient). Similarly, our experimental process did not circumvent analytical problems associated with potential autocorrelations (jackrabbit density data were frequently incorporated into calculations for determining other demographic variables). Ultimately, there seem few alternatives to perturbing predator numbers to assess the impact they are having on prey demography.

By its very nature, predation functions near the top of the trophic structure, with a variety of factors operating simultaneously at lower trophic levels influencing predatory interactions. Predator-prey interactions reflect complex accumulations of relationships as well as chance events. As a result, understanding predator-prey interactions requires a realization of the scope of events influencing predator-prey interactions, as well as taking them into account in scientific inquiries into predatory relationships.

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